

The Growth of the Slider Turtle, *Pseudemys*
scripta elegans

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Fred R. Cagle

Introduction

The naturalist's fragmentary knowledge of the habits and life history of turtles has been only feebly augmented since the days of Agassiz. The modern herpetologist has no thorough knowledge of the ecology of any one species and little or no information is available on the bionomics of many others.

In 1939 a long term program designed to collect data on the turtles of Illinois was initiated at Carbondale, in the southern part of the state, and data have been accumulated on many phases of the life histories of the more abundant species. In an attempt to obtain data on growth, longevity, attainment of sexual maturity, migration, home ranges, and associated problems, approximately 3000 turtles have been marked and released, and about 500 of these have been recovered at least once. Several hundred stomachs and gonads have been preserved for the study of food and for the analysis of the sex cycle.

The present report, concerning growth in the slider turtle *Pseudemys scripta elegans* Wied, represents the first segment of a long term program on the bionomics of this form. The primary purposes of this paper are: (a) to present and evaluate techniques for studying absolute growth in turtles and (b) to summarize our knowledge of the growth of the turtle named in southern Illinois.

Review of the Literature

Agassiz (1857) was the first to study the growth of turtles. On the basis of a few data on two species of *Chrysemys* and many years of observation on turtles, he suggests that the growth of turtles is exceedingly slow and that among the reptiles they are the slowest to attain sexual maturity. He concluded that females of the painted turtle do not begin to lay eggs until they are 10 to 11 years of age (1857:290). He also presents the record of a snapping turtle (*Chelydra serpentina*) that grew only one inch in 45 years.

This evidence supports the common opinion that turtles grow slowly and that they have exceptional longevity. The latter fact is further attested by Flower (1925:978), who shows that at least four species of *Testudo* have age records of 100 or more years.

The work of investigators since Agassiz show that turtles may on occasion grow rapidly. The most substantial of these studies have been made on turtles in captivity. Mitsukuri (1905:265) states that the Japanese soft shell (*Trio-*

¹ A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan.



nyx japonicus) may reach sexual maturity in about six years. The series of reports by Coker, Barney, and Hildebrand on the culture of the diamond-back terrapin (*Malaclemys*) at Beaufort, South Carolina, indicates that the males may be sexually mature when only three and one-fifth inches in length and that females may be mature at a length of four and three-fourth inches or an age of four years. Hildebrand (1932:559) states that terrapins maintained under similar conditions may show wide differences in growth, some being nearly full grown in five or six years, while others require twelve to fifteen years or longer to reach full growth. He further states (1929:70) that after an age of 8 to 10 years it attained, growth is so slow that it is almost negligible.

Pearse (1923) made the first important analysis of growth in turtles living under natural conditions. In his report on the marking of 406 painted turtles (*Chrysemys picta bellii*) in Lake Mendota, Wisconsin, he shows that the turtles increase their length and weight 73 per cent in the second year of their life (first season of growth), 31 per cent in the third year, and 25 per cent in the fourth and fifth years. In subsequent years the rate varies from 5 to 3 per cent.

Pearse attempted to correlate growth with age, but Hubbs (1924) notes that he failed to indicate how age was determined. The records of Pearse further demonstrate much variation in growth in individuals of about the same size.

Benedetti (1925) reports that the growth rate of *Testudo graeca* varies with the size of the individual, the sex, and the seasons of the year. Townsend (1937), in summarizing his notes on the growth of Galapagos tortoises (*Testudo vicina*) retained in colonies, states that 8 individuals housed at Houston, Texas, increased an average of 137 lbs. each in 8 years and approximately doubled the carapace length.

Sergeev (1937) studied the growth of *Emys europeae* and concluded that: (a) the growth is exceedingly variable, (b) the growth is rapid in juveniles but ceases completely in old individuals, and (c) the attainment of sexual maturity does not result in a slowing of growth. Liu and Hu (1940) conclude that the growth of *Geoclemys reevesii* is rather rapid and constant during the first five years but irregular and slow afterwards. They suggest that this slowing of growth may be due to the attainment of sexual maturity.

Parker (1929:371), in summarizing his discussion of growth in turtles, states, "It is clear from the evidence presented in this paper, that turtles, even large ones, may reach maturity at a comparatively rapid rate, and that the opinion commonly entertained of their great slowness of growth is scarcely justifiable. Without doubt their increase in late life is very slow and this may have given occasion for the belief in a low rate of growth in general. Such rates, however, do not apply to their early states."

The above citations represent the principal studies of turtle growth. There are many scattered observations in the literature of vertebrate zoology.

These past researches indicate, in general, that growth is much more rapid in juveniles than in mature individuals; that there is much individual variation in growth; and that turtles are rather long-lived vertebrates.

Methods

The ideal method of studying the growth rate of any animal is to make repeated observations at regular intervals on the same individuals living under the same natural conditions. Unfortunately, it is rarely possible to do this. The next best plan is to measure a large number of individuals and to study each one whenever and wherever it may be available. This procedure requires access to a rather large population, a dependable marking system, and an accurate method of measurement. Turtles have been collected and marked according to the latter plan since 1939 (Cagle, 1942:1944a).

Since I was interested in: (a) relative and absolute growth of the carapace and plastron, (b) secondary expressions of sexual maturity, (c) size and age groups, (d) possible value of the use of growth rings in growth analysis, and (e) determining which of the measurable structures were most reliable as growth indicators, the following set of measurements was selected:

Carapace length	Maximum length of carapace
Carapace width	Maximum width of carapace
Plastron length	Maximum length
Plastron width	Maximum width of posterior lobe
Height	Maximum height
Preanal region.....	Length from posterior edge of plastron to anterior lip of anus
Postanal region	Length from posterior lip of anus to tip of tail
Third claw	Length of third claw taken in straight line from base to tip
Plastral annuli	The maximum length of each annulus on the plastral plates. (pl. 2)

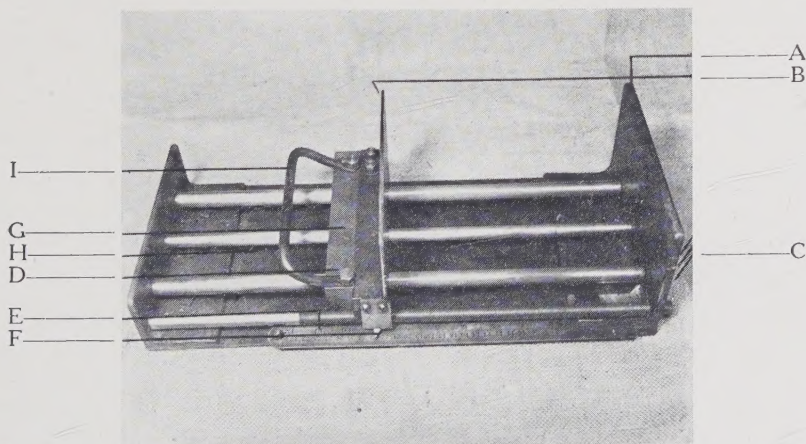


PLATE 1.—The measuring device. A turtle was measured by placing it against the fixed plate (a) and moving the sliding plate (b) until it was in contact with the turtle. The marks (c) indicate the points at which the carapace or plastron should come in contact with the plates. Once the sliding plate was in position the steel spring (d) was depressed and the measurement read from the rule (e) as indicated by the pointer (f).

The movable plate is attached to a heavy steel bar (g) sliding on steel rods (h) which penetrate it. The handle (i) makes it possible for the operator to more adequately control the pressure with which the plate is pushed against the turtle.

After much experimentation a steel measuring instrument was devised (pl. 1). This instrument consists of a heavy $\frac{1}{4}$ inch steel base on which are mounted 3 steel rods each $\frac{1}{2}$ inch in diameter. A vertical plate at one end serves as the fixed point in the device. Opposite this there is a sliding plate mounted on a $1\frac{1}{2}$ square steel bar pierced by the rods. The holes in the bar and the rods were fitted so closely that an oil film had to be maintained on the rods to allow movement. An adjustable metal pointer affixed to the steel bar moved above a standard metal rule marked in millimeters. A rod cut with millimeter threads was fixed to the base and the pointer was attached to a piece of spring steel permitting the pointer to deviate slightly to either side. A short section of rod cut with millimeter threads was fastened to the underside of the spring so that when the pointer was depressed the threads engaged the rod mounted on the base and thus moved the pointer to either the right or left, automatically indicating the nearest millimeter. A turtle to be measured was held at the proper point² against the fixed plate and the movable one pushed gently forward until contact was made. The measurement was read from the metal rule to the nearest millimeter. Marks on both vertical plates indicated the points for placing the carapace and plastron for measurement.

Young turtles on account of the flexible carapace and plastron, were measured with a more delicate instrument, the vernier caliper. This was also used in making the preanal, postanal, and third claw measurements.

Although weights were taken of many individuals, they were not regarded as of great significance because of the great weight of water irregularly carried by the turtle and the weight of the feces, which in some instances amounted to one-tenth the total weight of the turtle.

The growth rings of the plastron provided a second source of data for growth analysis. In a growing individual, these are formed at intervals on each of the plastral plates and provide a means of determining a portion or all of the growth history of an individual.

PROCEDURES IN RELEASE AND RECOVERY

All turtles were removed to the laboratory within a few hours after capture, where they were measured, marked, and photographed in color. Those not detained for stomach or gonad studies were then returned to the lake or stream from which they were removed.

THE AREAS STUDIED

These investigations were conducted in two principal areas, the Carbondale City Lake with its associated ponds and a segment of the drainage ditch system of the Mississippi flood plain. Population samples for comparative studies have been taken from many other lakes, ponds, and streams of southern Illinois.

City Lake is about three-fourths of a mile long and one-half mile wide with a maximum depth of 25 feet, average depth approximately 5 feet. As a

² A serious amount of error is introduced if extreme care is not taken to make all measurements in identical planes.

result of activities of the city water company, there is little aquatic vegetation and much of the shore line has been stripped of plant growth, thus eliminating much of the invertebrate life. The game fish are few and the lake is dominated by large, rough fish. Few basking sites and few favorable feeding areas are available for turtles.

Immediately adjacent to City Lake there are 3 small, artificial ponds. Thomas Pond is a small, clear-water pond, approximately one acre in extent, with a rich fauna and flora. The other two are typical, small stock ponds with clay shores and bottoms.

Within a radius of one mile of City Lake there are 3 other permanent water bodies. The largest of these is Thompson Lake, an artificial lake rich in plants and animals. Lake Ridgeway is a small pond on the college campus. To the south of Lake Ridgeway is the state pond located on the property of the state farm. Piles Fork Creek, a small stream running near the state pond and thence to the overflow of City Lake, is dry throughout much of the year but does provide a highway for turtles moving between these water bodies and City Lake (Cagle, 1944b).

The second general region, a segment of the drainage ditch system of the Mississippi flood plain, consists of a main ditch approximately 7 miles long and 2 principal tributaries each about 4 miles long. These ditches, constructed to drain the swamps of the region, are 15-30 feet deep and 20-50 feet wide at the top. During seasons of normal rainfall the main channel and lower reaches of the tributaries contain several feet of water and support a lush growth of aquatic vegetation and a large population of vertebrates, most of which move into the ditches from the river sloughs. During drought seasons these ditches dry up, forcing the aquatic life to aestivate or move long distances down the dry channel to the river (Cagle, 1944b).

The Annual Activity Cycle

The interpretation of the growth records depends on a knowledge of the annual activity cycle. It was essential to determine the limits of the growing season—when *Pseudemys* becomes active in the spring, takes its first food, shows the first evidence of new growth, and becomes quiescent in the fall. The necessary answers to some of these questions were obtained by sample trapping; by field observation of feeding, courtship, and basking; by examination of gonads and stomachs; by analysis of growth ring and recovery records; and from temperature records and experiments.

The temperature records promised to yield the most satisfactory means of defining the growing season. Unfortunately, scant information is available on the minimum and maximum temperatures at which turtles become or remain active. Baldwin (1925:443) found that neither the snapping turtle (*Chelydra serpentina*) nor the painted turtle (*Chrysemys picta*) could withstand a body temperature of 102°-105° F. (39-41° C.) for as long as thirty minutes and that individuals of both species become relatively inactive at temperatures below 50° F. (10° C.). Hildebrand and Hatsel (1927:376) report that 2 of 3 loggerhead turtles confined in an enclosure were frozen to death when the air temperature dropped to 26° F. (-3.3° C.), the third surviving down to

13° F. (-10.6° C.). Casual observations have been made by others on turtles moving about in ice-covered lakes, thus evidently at temperatures between 0° and 4° C.

Some work was undertaken to secure data basic to determining extremes of environmental temperature limiting the normal activities (maximum and minimum effective temperature) on the assumption that little or no growth occurs beyond the extremes. Field records were made of air and water temperatures at the time turtles were observed with subsequent study of the correlation of basking, feeding, and courtship with temperature; the rate and extent of temperature increase in basking turtles were studied and laboratory observations of turtle activity were made for various water temperatures.

No thermocouple or thermostat was available and the improvised procedures were accurate only to about 1° C. The temperature of individual turtles was taken by inserting a thermometer one-half to 2 inches into the cloaca for 3 minutes. Water and air temperatures were taken with the same thermometer.

In one experiment a juvenile female, 110 mm. in plastron length, was placed in a container of water in a refrigerator unit. At 8:45 A.M. when the turtle was placed in the water its cloacal temperature was 21.3° C., the water temperature 13° C. The turtle was quite active and moved rapidly about in the container when disturbed. One hour later the water temperature was 7.8° C., the cloacal temperature 19.3° C. When disturbed, the turtle executed slow swimming movements. Two hours later the water temperature was 3.4° C., the cloacal temperature 5.7° C. and the turtle reacted only feebly to external stimulation. It did not attempt swimming movements but merely tried to retract its head and feet into its shell. After 9 hours the turtle was found with the feet and tail frozen in one-quarter inch of ice. It did not react to any stimulus applied and was assumed to be dead; but when placed in cool water, it recovered without any apparent ill effects.

This crude experiment suggests that the minimum effective temperature for the species is about 10° C. as at this point swimming movements were so slow as to be ineffective. It supports the popular belief in the ability of turtles to withstand freezing temperature for a short time.

The basking experiments were performed to gain information on the absolute maximum body temperature. It should be pointed out here that under normal conditions the turtle experiences the minimum effective temperature in the water habitat and the maximum while exposed to the direct rays of the sun.

In a preliminary experiment a large female was placed in bright sunlight with the plastron turned upward. Although not the normal basking position, it discouraged the turtle from making attempts to move about and made cloacal insertion of the thermometer simpler. Cloacal readings taken at irregular intervals showed an increase from 17° to 37.2° C. in 180 minutes (Fig. 1). When the cloacal temperature reached 34° C., the turtle was quite active and made strong attempts to escape. It continued those endeavors until its temperature reached 37.2° C., when all movements became convulsive and the turtle was removed to a cool place, where it recovered.

That turtles can survive such high temperatures is indicated by one field experience. In June, 1941 a drainage ditch south of Dixon Springs, Illinois, was checked for turtles. The water was very low and was distributed in scat-

tered pools a few inches to a foot deep. In one of the shallow, gravel bottomed pools in which the water temperature was 37°C ., the turtles were very active. Those that could ordinarily be handled carelessly with impunity, snapped and scratched viciously when caught. Three species, *Chrysemys picta* ssp., *Pseudemys scripta elegans* and *Kinosternon subrubrum* ssp., were taken from this pool.

In a second experiment, 5 turtles that had been out of water for several hours were placed in the sun and cloacal temperatures taken at 5 minute intervals. The air temperature was 18.8°C ., and cloacal temperatures ranged from 13.9°C . to 15°C . All were quite sluggish to begin with but their response to the insertion of the thermometer became more pronounced as the temperature increased. When 18°C . was reached the turtles appeared to be normally active. The cloacal temperatures increased 12.4° to 14.9°C ., mean increase 13.5°C ., in 168 minutes, i.e., to 28.8 to 30°C . None of the turtles showed any evidence of discomfort (fig. 1).

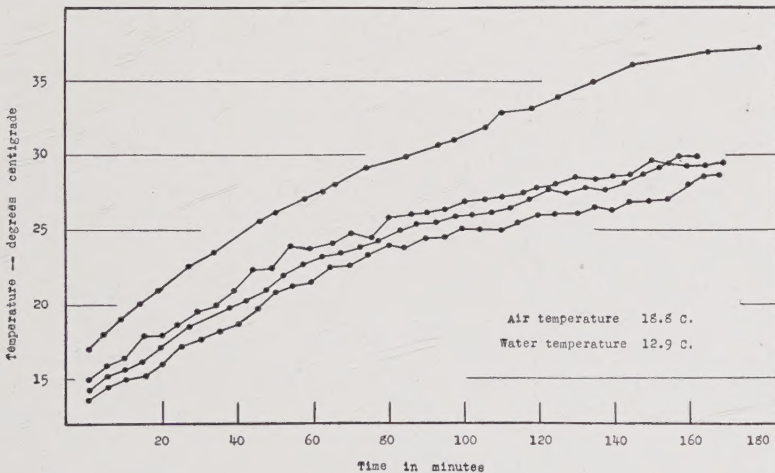


Fig. 1.—The rate of temperature increase in four turtles exposed to direct sunlight.

These experiments suggest that the maximum effective temperature is about 37°C ., that the optimum temperature is between 18°C . and 30°C ., that the temperature of a basking turtle may increase rapidly, and that the length of a basking period is determined by the water and air temperature and the intensity of the sun's rays. These experiments are crude but it appears logical to infer that the period of normal activity in nature is limited within the internal temperature range of approximately 10° to 37°C . The turtles doubtless do not feed beyond the extremes of this temperature range and consequently do not grow.

Since it has been demonstrated (Baldwin 1925:432) that the difference between internal temperature and environmental temperature fluctuates only from 1.5°C . to 3°C . within the non-critical range, I deduce that spring activ-

ity begins when the temperature reaches approximately 10° C. and that fall quiescence is initiated when the water temperature returns to the same level.

Field studies formed the most satisfactory basis for an outline of the activity cycle. Traps of two types, box traps and 3 hoop, single-throat nets were run at irregular periods in City Lake over a three year period and records of the number of turtles caught per hour in each set recorded (Fig. 2). Turtles were collected in each month except December, January and February. The trapping records indicate that the peaks of activity are reached in May and September with a decline during June and July. The activity peaks correspond with mean monthly water temperatures of 21.7° C. (71° F.) and 25° C. (77° F.) and the decline in activity with high water temperatures. Other observations substantiate these conclusions.

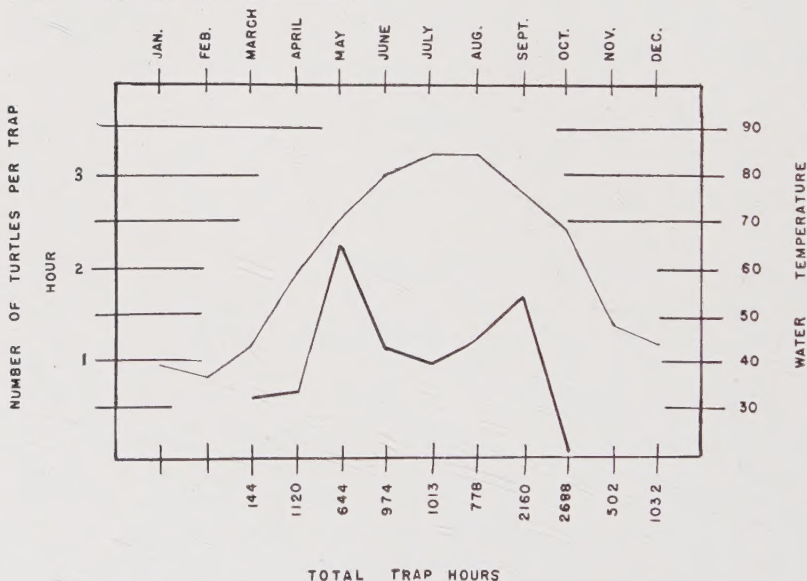


Fig. 2.—The annual cycle of activity. The upper curve indicates the mean monthly temperatures during 1940; the lower curve, the number of turtles per trap hour in each month.

No *Pseudemys* was observed in January although the lake shore was scouted many times and traps were set on several occasions. That all species of turtles were not inactive at this time is shown by the fact that 9 examples of *Chrysemys* were collected from a mine pond in January, 1938, where the water temperature was 11.1° C.³

Three live turtles were found on the shore during the warmer days and 14 juvenile turtles were collected from shallow water in February. None of the

³ Conant (1938:149) states that painted turtles (*Chrysemys*) were collected during every month of the year in the Toledo Ohio area and were frequently observed moving about under the ice.

turtles collected in the water were moving about and those basking made no attempt to retreat to the water. One of the 14 juveniles was seen through $\frac{1}{2}$ inch of ice and was so sluggish it did not escape while the collector broke the ice to reach it. All of the stomachs were empty.

One of the basking turtles collected from the shore made no movement when picked up. The limbs were completely relaxed and the anus remained open after the thermometer used in taking the cloacal temperature (13° C.) had been removed. Another turtle collected from a similar situation made no move to escape; it simply pulled in its head and legs when touched. Its cloacal temperature was 12.8° C.

On the warm days of late March when the air temperature rises above that of the water, occasional turtles may be observed but no mass basking occurs. Turtles are easily collected from shallow water during March; the water is still not warm enough to allow more than feeble movements but the turtles appear to be restless and wander slowly about the bottoms. Turtles were frequently collected on shore or from basking sites where they had apparently dallied so long that they had become too numb to return to the water. None of those collected in March contained food in their stomachs although crayfish, tadpoles, and dead fish were observed along the shore in relative abundance.

Throughout April there is an increase in activity. Numbers of turtles may be seen at the basking sites and the first evidences of spring courtship behavior may be noted. On April 20, 1940, 163 basking turtles were counted within 100 feet of an observation tower and courtship was repeatedly observed.

May, June and July field data indicate that the turtles are in the height of the courtship activity during May. Feeding activities were observed during these months and basking turtles were numerous on every warm day.

During late August and early September courtship behavior again was the most prominent activity observed. Many of the ponds, lakes, and streams reach low levels in September; the water becomes quite warm and many individuals move overland long distances from one body of water to another (Cagle, 1944b).

In October one notes a slackening in the activity of the turtle. Observations indicate that water temperatures are so lowered that most turtles seek hibernating quarters or simply settle to the bottom in shallow water where they probably remain until warmed by the spring sun.

A large number of turtles was collected in a cypress slough near Cypress, Illinois, in October, 1939. The turtles had burrowed into mud and debris at the edges of shallow pools in the swamp or had crawled into the hollow decaying cypress stumps, where some were literally stacked in layers. All were quite sluggish and all of 40 stomachs examined were empty. The water temperature was 10° C. on October 22, 1938, when 42 turtles were taken from a cypress stump from which 10 had been taken on a previous day.

During November turtles show little activity. A few individuals were collected from the mud flats at City Lake and on some days turtles were observed basking. Field observations in November 1939, indicate no activity when the water temperature was 10° C. or less but at 3 different times when water

temperatures were 12.8°, 12.8° and 15° C., turtles were moving about in the water and some were basking. On November 25, 1938 one large male of *Pseudemys* was observed moving feebly under the ice on a small pond. The water temperature was 2.7° C.

Turtles collected during December from the mud flats of City Lake were inactive and their stomachs contained no food. Turtles were observed basking on logs in December.

These field observations indicate that the turtles cease feeding in October and are active only as the water temperatures permit during the winter months. The first considerable amount of basking occurs in March, but there are no great numbers of individuals at basking sites until the last of April and the first of May. There is no appreciable basking activity when the water temperature is less than 10° C., but when the water had reached 12° to 15° C., three turtles were observed moving about in the water and basking. It is probable that the minimum effective temperature for *Pseudemys* and perhaps other turtles as well is approximately 10° C.

On this assumption turtles would begin their activities about the middle of March and end them during the latter part of October. This is verified by the fact that the first trapping returns were obtained in March and the last in October. The activity curve for *Pseudemys* based on the number of turtles collected per trap hour corresponds well with one prepared by Conant (1938) on the basis of the number of specimens brought to the Toledo Zoological Park in each month. His records show that turtles are comparatively inactive from October to March, a total of only 33 being collected in that period as contrasted with a total of 354 in the other months. From March there was a monthly increase in the number of turtles reported to a maximum in June with a subsequent decline. Conant's graph indicates that the first large collections were made in April when the mean monthly temperature was approximately 48° F. (8.89° C.) and the largest number was reported in June when the temperature was approximately 72° F. (22.2° C.). In October, when there was a decided reduction in the number of turtles collected, the temperature was approximately 53° F. (11.7° C.).

The optimum environmental temperature for *Pseudemys*, from examination of the activity curve, appears to be about 21° C. (70° F.), as both peaks occur at that water temperature (Fig. 2).

The period of egg laying falls within the first activity period. Thirty females containing eggs ready to be laid were collected in May, June, and July during the four years of study. Females were seen depositing eggs during May and June, and many nests were found in early May.

From all of my observations the growing season must fall essentially within the period from late April to early October.

Other workers have similarly defined the period of activity for other species. Hildebrand (1932:553) reported that the annual active feeding period of terrapins is comparatively short. The animals are seldom continuously active and feeding regularly before the first of May and by the middle of October they become inactive and cease feeding. He states, "The animals are so sensitive to temperature that even during cool days in mid-summer their capacity for food consumption is markedly reduced."

Butler (1885:37) notes that the box turtle enters the ground in southern Indiana during the latter part of September or early in October. Penn and Pottharst (1940:27) state that the box turtle (*Terrapene carolina*) entered hibernation when the temperature dropped to near 65° F. (18.3° C.). Conant reports that of 182 spotted turtles (*Clemmys guttata*) 12% were found in March, 28% in April, and 40% in May. Risley (1933:690) states that the earliest collections of musk turtles (*Sternotherus odoratus*) were made in late March. Everman and Clark (1920:607) state that the map turtle (*Graptemys geographica*) does not hibernate but is active all winter and may be observed through the ice walking about on the bottom. Abbott (1884:37) who observed 9 species of turtles concluded that there is considerable winter activity, even when they are not feeding.

These reports of winter activity indicate, as would be expected from the lag in temperature change of water, that the terrestrial turtles begin hibernation earlier than aquatic ones in the same area. My own observations indicate that turtles may move about at air temperatures as low as 15° C. It also appears that the minimum effective temperature is not the same for all species. Cahn

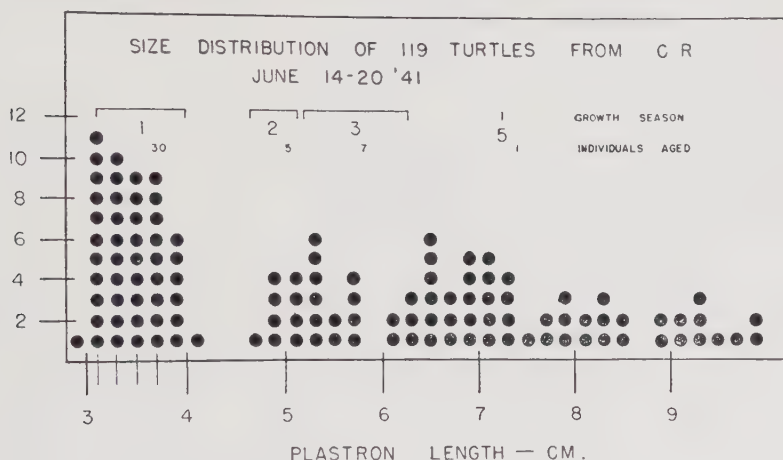
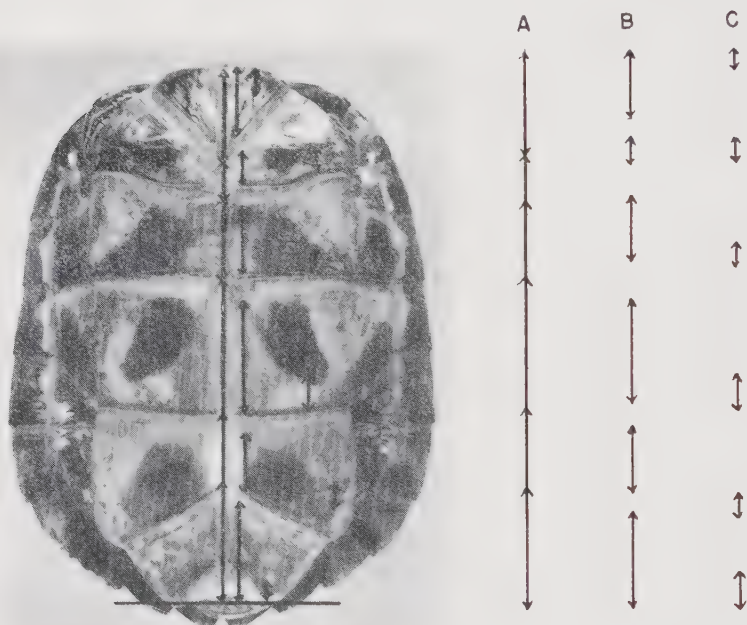


Fig. 3.—The size distribution of 119 turtles collected from City Lake, June 14-20, 1941.

(1937:102) observes that *Terrapene ornata* enters hibernation about 2 weeks earlier and remains there nearly a month longer than *Terrapene carolina*. He further reports that *Chrysemys*, *Chelydra*, and *Terrapene* enter hibernation in sluggish active through the winter in southern Illinois and enters hibernation during October in the northern part of the state.

The growth records of turtles released and recovered offer a more accurate definition of the growing season. The majority (87 out of 104) of the turtles in the size range 20-100 mm. released for any substantial part of the period from May 1 to October 1 shows some growth, but none of those at liberty October and emerge about mid-April; but he suggests that *Graptemys* remains only during the period of October 1 to May 1 grew at all.

Some of the turtles recovered after being released for comparatively short periods during the growing season had grown rapidly. This was particularly true of turtles in the 20-50 mm. group. No. 2337, released for 62 days, increased 7 mm. in plastron length. No. 2512, released for 78 days, grew 10 mm.; No. 2513 grew 7 mm. in 26 days; No. 2514 grew 16 mm. in 78 days; No. 2627 grew 14 mm. in 55 days. Turtles released within the period October 1 to May 1 and those released for part of the growing season and the winter season exhibited much less growth. Two individuals at liberty during two winters and the growing season of 1940 grew approximately the same



Σ A—Present plastron length.

Σ B—Plastron length at first of growing season.

Σ C—Plastron length at first of previous growing season.

PLATE 2.—The method of measuring growth rings. The length of each ring is measured between the points indicated by the black arrows, and the sum of the lengths of the rings in each set used as the plastron length at a time determined by the date of collection and the condition of the growth zones.

For example, this individual, collected June 12, 1941, has two distinct sets of growth rings, the smaller of which (c) indicates the size of the birth plates. Since the turtle was collected near the middle of its growing season and the last-formed growth zone is conspicuously lighter than the other, we may conclude that the last zone represents growth made during the season of 1941. Further, in view of the presence of birth plates we may conclude that the turtle is in its second season of growth.

The amount of increase in plastron length for this first season may be obtained by subtracting the sum of (c) from the sum of (b); the growth for the second season (43 days in the season of 1941), the sum of (a) minus the sum of (b).

amount as four released only in the 1941 growing season; in other words, growth was limited to the growing season.

Growth zone measurements (pl. 2) also indicate that the first growth of the season occurs in May, and that growth is continuous to October. Turtles collected in May were the first to show distinct growth zones forming (fig. 4). The mean growth for each month shows a steady increase to October, when, with the exception of a single September record, the peak is reached. Variation is to be expected in the length of the growing season as a result of fluctuation in such factors as temperature, food, and water level. Juvenile turtles collected in mid-growing season frequently showed no growth. Of 129 turtles collected from the mudflat at City Lake, June 14-20, 1941, 86 had not grown so far that season, 25 had grown slightly, and 18 exhibited conspicuous growth.

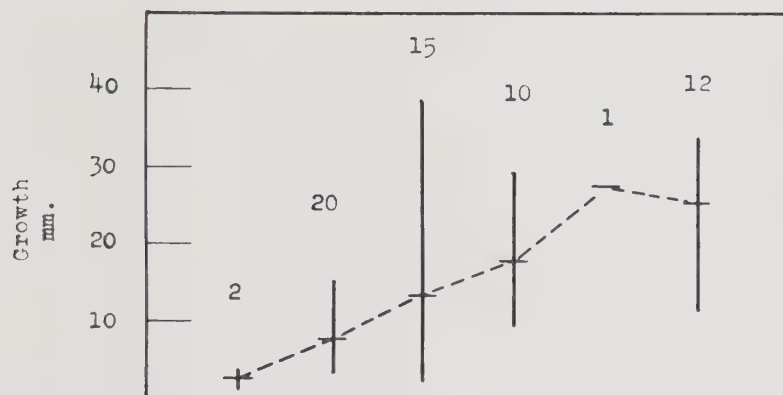


Fig. 4.—The monthly growth increment of turtles in their first season of growth at City Lake.

Hildebrand (1929:45) states that young terrapins "do not feed regularly until about the latter part of May and do not make perceptible growth for a month or more after regular feeding takes place."

These combined observations indicate that growth begins in May and ends in October; arbitrarily, as a matter of convenience, this period will be hereinafter considered as extending from May 1 to October 1.

Use of Plastral Annuli in Growth Studies

The borders of the scutes of most turtles are margined by grooves that have commonly been called growth rings. Since the term "annuli" has been widely accepted for the similarly formed rings in fish scales, it will be convenient to use it here; I have used "growth ring" and "ring" as alternates. The

study of these annuli in *Pseudemys* promised a method of determining age and a supplementary method of studying growth. It soon became apparent that the accumulation of growth data through the study of marked turtles would be slow and cumbersome and some additional means of growth study was sought.

The annuli are slight indentions in the horny plates, impressed also on the underlying bone. The shape of the groove varies considerably in individual turtles and in successive years. In some instances it is steep-sided and deep and in others wide and shallow, probably a reflection of growth conditions. The annuli bound each plate of the carapace and plastron. In some species that do not shed their horny plates, they remain visible until they are worn off. In those that do shed, the rings fade with each successive shedding and there are rarely as many as five rings visible.

Investigation on other species of turtles throws light on the value of the annuli for age determination. Ewing (1939:90) indicates that in *Terrapene carolina* they are produced by the slower and more irregular formation of the horny substance during the period of hibernation. Townsend (1937:290) points out that the tortoises (*Testudo vicina*) housed in the winter developed a conspicuous white growth zone when turned out on grass in the spring. He states, "This treatment produced a new ring each year, indicating age; growth slow in winter, rapid in summer. Tortoises in southern Florida, having access to grassy ranges at all times, were never lacking a faint whitish ring. However, tortoises of similar size and weight had equal numbers of rings, regardless of treatment." He further indicates that the rings are valid growth indicators in the younger animals but that it is difficult to count rings in the older ones.

Nichols (1939:16), referring to *Terrapene carolina*, shows that the first 5 or 6 annuli are probably added regularly, one each year, and later on years are missed with increasing frequency. He found that in 5 turtles the number of annuli added corresponded exactly with the number of years released. One turtle added only one in 8 years; another only 2 in 7 years. It is of importance to note that all turtles adding few annuli as compared with the number of years released were more than 6 years old and 2 were more than 13. Three individuals added one more annulus than the number of years released.

Miller (1932:195) studied the changes in the third vertebral scute of a number of desert tortoises (*Gopherus agassizii*) kept in captivity. He found that the annuli formed at the margin of the hatchling scutes retained their original dimensions even though the turtle had doubled in size, but that study of known two-year-olds and of larger animals of unknown age proved that formation of annuli may be irregular. He points out that this is what might be expected in the desert where growth conditions fluctuate; but under animal house conditions, where the food supply is continuous and temperature the dominant influence, the annuli are still irregular and do not accurately reflect seasonal activity.

Hildebrand and Hatsel (1926:13) find that the annuli are reliable age indicators in the younger diamond-back terrapins, but not in mature specimens, and Risley (1933:703) comes to the same conclusion for the musk

turtle. Benedetti (1925) in a study of *Testudo graeca* could determine the age of only 94 of 340 individuals through the use of annuli.

Obviously the value of the annuli as age indicators varies not only with the species but also with the habitat occupied by the individuals in question. Any interruption in the supply of food or ability of the individual to utilize food might result in the cessation of growth and the formation of an extra annulus or in none being formed for a given season. A turtle might remain in a pond for several weeks after it has become completely barren of food and then move to another area where food is abundant, and this might result in the formation of an annulus. There is ample evidence to indicate that some individuals may not grow for several seasons and may not form annuli.

Pseudemys presumably is subject to the same sources of irregularity of its annuli as are other turtles. An occasional specimen exhibits a weakly defined annulus that might well represent a temporary cessation or slowing of growth during the growing season.

The first annulus is formed in *Pseudemys* of southern Illinois by the cessation of growth during the first winter of life and the subsequent rapid growth during the first season. Since during the progress of the growth research no hatchling turtles were observed to grow during the interval between hatching and the beginning of the first period of winter quiescence, it is apparent that the first annulus marks the boundaries of the birth plates.

As long as this ring is visible one may reasonably assume that all the annuli ever formed are present but once it is lost the assumption can no longer be safely made. This first annulus in *Pseudemys* is rarely visible after 3 years; of 56 turtles retaining it only one had more than 4 annuli.

However, the annuli would be of much importance in growth studies if it could be demonstrated that: (a) in most individuals not more than one is formed annually, (b) the zone between any 2 annuli represents one season of growth, (c) the approximate period of time represented by any area between rings is determinable.

The only satisfactory method of checking points (a) and (b) was to compare annuli on individuals at the time of release and the time of recovery.

During 3 years the measurements of the annuli on the plastral plates of 28 *Pseudemys* were taken at both the time of release and the time of recovery (Plate 2 and table 1). These data indicate that the annuli are formed annually and that the area between any 2 annuli represents one season of growth. For example: No. 215, when collected July 27, 1939, had 3 sets of annuli visible, the largest of which totaled 113 mm. in length, theoretically the plastron length at the end of the 1939 growing season. This turtle was again taken on September 17, 1940—approximately 14 months after its release. If annuli are formed during the period of hibernation, this turtle would be expected to have added one set during the interval of release. When the plastron was examined only two annuli were found; the smaller, measuring 112 mm., was undoubtedly the same set that was present in 1939; the larger, measuring 123 mm., was the one formed during the winter of 1939-40. Two annuli had been lost. Evidently the annuli fade rapidly. All the other turtles growing during the release period formed one annulus for each winter period released (table 1).

TABLE 1.—The comparison of annuli at time of release and recovery.

No.	Date collected	Sum of lengths of annuli (plastron length at the end of the season indicated)					
		1936	1937	1938	1939	1940	1941
215	7/27/39	99.2	108.3	113.0	-----	-----	-----
	9/17/40	-----	-----	112.0	122.8	-----	-----
217	7/27/39	-----	89.5	100.7	-----	-----	-----
	8/21/39	-----	-----	101.2	-----	-----	-----
232	7/27/39	31.2	41.4	54.5	-----	-----	-----
	9/ 1 /42	-----	-----	-----	-----	-----	80.4
236	7/28/39	-----	-----	96.1	-----	-----	-----
	5/ 3 /41	-----	-----	-----	107.3	-----	-----
244	7/30/39	-----	-----	111.4	-----	-----	-----
	4/25/41	-----	-----	-----	-----	126.5	-----
246	7/31/39	-----	-----	137.7	-----	-----	-----
	8/ 6 /41	-----	-----	-----	-----	143.5	-----
269	8/ 9 /39	-----	97.0	107.0	-----	-----	-----
	8/11/41	-----	-----	-----	110.9	119.8	-----
273	8/ 9 /39	-----	52.2	64.5	-----	-----	-----
	5/ 3 /41	-----	-----	-----	75.3	84.4	-----
275	8/ 9 /39	72.8	80.7	91.1	-----	-----	-----
	9/11/42	-----	-----	-----	-----	87.8	98.6
289	8/11/39	-----	99.7	112.2	-----	-----	-----
	8/14/41	-----	-----	-----	-----	134.2	-----
297	8/11/39	99.6	113.3	126.6	-----	-----	-----
	4/23/41	-----	-----	128.3	138.9	150.7	-----
299	8/11/39	-----	-----	145.0	-----	-----	-----
	8/ 5 /40	-----	-----	-----	150.7	-----	-----
301	8/11/39	110.7	121.3	126.2	-----	-----	-----
	8/ 6 /41	-----	-----	-----	132.5	148.1	-----
315	8/11/39	-----	106.6	119.5	-----	-----	-----
	8/ 1 /41	-----	-----	-----	128.7	137.1	-----
318	8/11/39	-----	101.0	113.1	-----	-----	-----
	5/ 6 /41	-----	-----	-----	125.0	132.1	-----
356	8/26/39	-----	76.1	83.6	-----	-----	-----
	8/18/40	-----	-----	-----	92.6	-----	-----
369	8/26/39	-----	93.6	105.6	-----	-----	-----
	5/18/40	-----	-----	-----	107.7	-----	-----
497	5/19/40	-----	99.3	116.6	-----	-----	-----
	4/25/41	-----	99.6	113.8	131.0	135.2	-----
544	5/18/40	-----	81.9	90.8	-----	-----	-----
	5/ 5 /41	-----	-----	-----	94.5	99.6	-----
638	6/30/40	-----	-----	-----	30.0	-----	-----
	5/23/41	-----	-----	-----	31.9	50.5	-----
664	7/ 2 /40	-----	-----	84.8	97.1	-----	-----
	5/ 3 /41	-----	-----	-----	99.0	108.7	-----
665	7/ 2 /40	-----	-----	97.5	112.2	-----	-----
	5/ 1 /41	-----	-----	99.2	113.4	-----	-----
691	7/10/40	-----	-----	-----	30.5	-----	-----
	5/23/41	-----	-----	-----	-----	45.1	-----
719	7/27/40	-----	-----	87.4	100.4	-----	-----
	8/ 6 /41	-----	-----	-----	-----	114.5	-----
728	8/ 3 /40	-----	-----	65.7	78.7	-----	-----
	5/22/41	-----	-----	-----	83.8	90.5	-----
813	9/18/40	-----	-----	-----	94.0	-----	-----
	8/ 6 /41	-----	-----	-----	-----	98.9	-----

See page 727 for key to abbreviations used in the above table.

A turtle that hibernates without having grown during the growing season can form no additional annulus. When growth is very slight, the annuli are close together and may even blend on some portions of the scute.

The area between two successive annuli, which may be designated as the growth zone, represents the growth for one season. The period represented by a particular growth may be determined by the date of examination and the appearance of the growth zone. In a turtle collected in July, the middle of the growing season, if the growth zone is light in color and covered with only a thin layer of horn, it may be concluded that the zone represents that season's growth. If the growth zone is well pigmented and covered with thick horn, it presumably did not represent growth during the season collected, but that of a previous season. New growth is easily detected and would only rarely be confused with growth made during an earlier period.

It remains to test the assumption that increase in the size of the plastral plates is by simple additive growth.

The simplest demonstration of this is the fact that annuli remain the same size once they are formed. Thus the annuli that form about the margins of the birth plates remain distinct in many turtles for several years and may easily be measured. Measurements made of the first formed annuli of 144 individuals varying in age from one to 5 seasons ranged from 23.1 to 35.0 mm., mean $30.8 \pm .18$ mm. For comparison, and also as further test of the validity of the annulus measurement method, the plastral lengths of 65 hatchlings 24 to 48 hours old were measured. The range of this measurement was 24.5-33.0 mm., and the mean, $29.8 \pm .24$ mm. Since the standard error is contained in the difference between the means only 1.6 times we may conclude that the first formed annuli had not increased significantly in length. This type of growth is further demonstrated through the close correlation of measurements taken of the same sets of annuli at intervals (table 1).

Although annuli once formed do not change in size, the repeated shedding of the scutes does cause them to disappear so that the number visible depends on amount of growth and the age of the turtle.

For determining growth from measurements of annuli, the sum of the lengths of the annuli (one on each plastral plate) is used as the plastral length of the individual at the time the annulus was formed, and the sum of the lengths of the plastral plates as the present plastral length. The difference between the two sums then represent the actual increase in length of the plastron during the period represented by the growth zone (pl. 2).

Sergeev (1937) has used the method, suggested by Lea for the determination of growth in fishes from study of scale dimensions, a technique now in

extensive use by ichthyologists. Sergeev used the formula
$$\frac{L_1 - C_1}{L_2 - C_2}$$
 where L_1

was the unknown, L_2 the length of the turtle, C_1 the length of the annulus, and C_2 the length of the scute in question. He used, experimentally, the annuli on various plates of the plastron and carapace of several species (*Testudo ibera*, *Emys europea*, *Chrysemys concinna*) and compared the results obtained by this procedure with the results obtained by the study of the sizes of turtles

of known age. He concluded that this method could be utilized in the analysis of growth of all those turtles that form annual rings.

This technique, a rapid and efficient method of making growth determinations, is in use in the growth research in Illinois. To date, the annuli of the pectoral plate only have been used and results have been satisfactory. Since it is apparent that there are some relative growth changes in the plastron plates, it is suggested that before the technique be used in growth studies the validity of the use of the plate selected be demonstrated in the species concerned (i.e., that the length of the plate retains a constant relation to the length of the plastron throughout the life of the individual).

The method as employed by Sergeev was used experimentally with *Pseudemys*. In 28 individuals it has been possible to compare the growth as determined by three methods: release-recovery, measurement of all plastral annuli, and computation from the measurements of pectoral scute annuli (table 2). In most of the individuals studied results from the three methods agree. No. 150, when released for 257 days in the growing season, grew 21 mm. Its growth as calculated for 306 days of the growing season on the basis of annulus measurements was also 21 mm. With few exceptions (see nos. 2396, 2412) the remaining records demonstrate the validity of the use of annulus measurements in computing growth.

In computing growth from annulus measurements, the length of the plastron must be considered as the sum of the lengths of the plastral plates and not as the overall length of the plastron. If the total length of the plastron is measured in one step and used in computing the growth, error will result, because of the slight curvature of the plastron.

The annulus measurement procedure may be used in conjunction with the release-recovery method to delimit the period in which growth occurred. Individual No. 236 (table 2), released July 28, 1939, and recovered May 3, 1941, increased the plastron length 2 mm. during that period. When collected May 3 measurements of the growth zone indicated that it had grown 2.9 mm. in the previous season of 1940. It may thus be concluded that this individual did not grow during the last portion of the 1939 season, the winter of 1939-1940, 1940-1941, or the few days it was released in the 1941 season.

Shedding of the Outer Layer of the Horny Plates

The time of shedding of the horny plates affects the annuli and may be correlated with growth. It is necessary to know when and how frequently shedding occurs, what effect it has on the annuli, and whether or not the shedding of the plates stimulates growth. Groups of turtles collected during each month were examined for evidence of recent, present, or near future shedding, and a number of individuals were marked with enamel on the carapace and released in the hope of recovery.

The chronological distribution of the records of shedding indicates that it takes place mainly in late summer but that it may occur during other periods. Some turtles were found shedding during each month in which adequate samples were taken (table 3).

Ewing (1939:88) states, "Many turtles at the time of molting cast the

TABLE 2.—Comparison of growth determinations as made by recovery records and annuli measurements.

No.	Sex	Dates of release and recovery	Total days released	Total days in growing season	Growth determined from recovery records	Days in growing season represented by rings	Growth determined from all plate annuli	Growth determined from pectoral plate annuli
					mm.		mm.	mm.
150.....	j	6/18/39-2/11/41	603	257	21	306	21	21
155.....	j ♀	8/19/39-6/30/40	315	103	9	61	9	8
212.....	j ♀	7/27/39-5/3/41	645	221	4	153	4	3
215.....	j	7/27/39-9/17/40	417	65	3	153	11	10
232.....	j ♂	8/1/41-9/1/42	396	184	29	123	27	27
236.....	j	7/28/39-5/3/41	644	220	2	153	3	2
244.....	j ♀	7/30/39-4/25/41	634	215	24	306	32	32
269.....	j ♀	8/9/39-8/11/41	732	308	9	103	9	6
273.....	j	8/9/39-5/3/41	632	208	6	153	7	8
310.....	j ♀	8/11/39-4/25/41	622	203	3	153	3	5
315.....	j ♀	8/11/39-8/1/41	720	296	6	193	8	6
318.....	j ♀	8/11/39-5/6/41	633	209	9	153	7	2
356.....	j	8/26/39-8/18/40	357	145	1	110	4	3
430.....	j	9/11/39-6/5/41	632	208	14	153	14	..
439.....	j	9/16/39-2/21/41	523	188	26	153	25	..
480.....	j	3/23/40-5/14/41	417	167	4	153	7	6
497.....	j ♀	5/19/40-4/25/41	341	134	3	153	4	2
544.....	j ♀	5/18/40-5/5/41	352	140	2	153	5	5
562.....	j	5/30/40-4/25/41	330	123	3	153	7	4
638.....	j	6/30/40-5/23/41	327	114	12	153	19	23
664.....	♂	7/2/40-5/3/41	305	93	2	90	2	..
691.....	j	7/10/40-5/23/41	317	105	6	153	7	8
719.....	j	7/27/40-8/6/41	375	163	8	98	9	10
813.....	j	9/18/40-8/6/41	322	110	7	98	5	5
1773.....	j	3/31/41-9/7/42	525	283	23	283	24	26
2345.....	j ♀	5/3/41-8/6/41	95	95	6	98	7	8
2396.....	j	5/14/41-7/3/42	415	203	26	68	19	17
2412.....	j	5/15/41-9/1/42	474	262	17	124	21	..

See page 727 for key to abbreviations used in the above table.

outer layers of the dermal shields. These usually come irregularly at the time of the general molt, which takes place in the early part of the summer. At times however, the old horny layers do not loosen and may not be cast for two or more years."

Of the turtles marked, painted with enamel on the carapace, and released,⁴

⁴ There is of course some possibility that the enamel on the carapace may interfere with normal shedding but as in some cases recovered individuals were molting enamel-coated plates with no difficulty, we may at least assume that the enamel does not prevent shedding.

none of 9 released in October of 1938 had shed during the release period, but 2, No. 30 and No. 15, were in the process when recovered. There was no paint present on the scutes of No. 15, and it was thus not certain that this was its first shedding since its release. No. 30, however, still retained paint on the molting plates. The seven turtles that did not shed were at liberty from 200 to 652 days. The turtles released July 10, 1940 and recovered in 1940 and 1941 were very different in this respect. Of 23 releases, 19 shed during the period of release, which varied from 24 to 397 days. The 4 turtles that did not shed were re-collected in the first few days of the following May. Two had shed just previous to the time of their release, but it was not possible to determine if the other 2 had recently shed.

TABLE 3.—The occurrence of shedding.

Month	No. not molting	No. molting	Per cent molting
January	0	0	0
February	18	0	0
March	1,101	102	8
April	28	0	0
May	251	3	1
June	451	17	4
July	65	21	24
August	310	24	7
September	27	13	33
October	120	11	8
November	5	0	0
December	0	0	0

See page 727 for key to abbreviations used in the above table.

These two sets of data indicate that shedding may occur more frequently in young turtles than in old, as all of the individuals released in 1938 had passed the stage of rapid growth but all of those, except possibly Nos. 675, 699, 700 and 695, released in 1940 were comparatively young turtles. Older turtles, furthermore, have thickened horny plates that are never found in the young.

This observation might lead one to the assumption that shedding is a function of growth of the shell, but such assumption is not clearly justified by the growth records. Only 11 of the 19 individuals that shed their plates in the interval of release showed actual increase in length, and 5 of 11 turtles that did not shed did show some growth. All 5 of these are in the first group (old turtles), and in the second group (younger turtles) the 4 that did not molt showed no growth.

Pearse (1923:147) suggests that differences in individual growth in *Chrysemys* are probably correlated with shedding, growth being thought to be rapid immediately after the plates are lost. There is no evidence in support of

this view from this present study. Of 14 turtles known to have shed near the time of capture, only 7 grew in the subsequent period of release. Thus, there appears to be little reason for inferring rapid growth immediately after shedding.

Shedding has no effect on the actual formation of the growth rings but does change their appearance. When the layer of epidermis extending over the entire scute, including the new growth zone, is shed, the outline of the rings formed in previous seasons is weakened. Successive shedding presumably accounts for the elimination of the growth rings in older turtles (pl. 3).

Analysis of Growth

Other students of growth in turtles have stated its amount in terms of increase in length of carapace or of total weight. These were found to be less satisfactory as a measure of growth in *Pseudemys* than increase in plastral length. The plastron appears to be less affected by changes in the height or curvature of the carapace than any of the 5 shell measurements made; and in addition the plastral annuli, formed in a closer approximation to a plane, are more usable as a measure of growth than those of the carapace. The plastral length is used here as a measure of the size of the turtle, and growth is discussed in terms of plastral length only.

Absolute growth in plastral length was determined through release-recovery records, annulus measurements, and measurements of the plastron. Measurements of annuli were made on 717 individuals; 621 juveniles, 42 males and 54 females. Of these, 177 had 2-4 rings representing 2 to 5 successive seasons of growth. Plastral length measurements were made on 2880 turtles. Of 1985 turtles marked and released, 466 were recovered 1-5 times, with a total of 603 instances of recovery.

In the method of release and recovery, an increase in length of 1 mm. or more is the minimum that can be detected. Turtles showing no increase in measurements may have grown a fraction of a millimeter, or not at all. Growth ring measurements could not, in most individuals, be used to measure an increase in length of less than 2-3 mm. A small increase in total length of the plastron makes such a slight difference in the individual growth zone of the component plates that they cannot be accurately measured. Thus the lowest point in the range of growth as determined by ring measurements must be expected to be higher than that determined by release-recovery records; and the percentage of turtles showing no measurable growth on the basis of plastral annuli will be greater than the percentage making no measurable growth as determined by release-recovery procedure.

As age cannot be determined adequately for most individuals, and no distinct natural size groups are apparent in turtles over one season old, growth must necessarily be discussed in terms of arbitrarily selected size groups of juveniles, males and females. The sex of juveniles cannot be satisfactorily determined without dissection, and they are here considered as a group.

The secondary sex characters of the male (elongated nails on fore foot, long preanal area, narrow head, melanism) do not appear until the individual reaches a length of 85-110 mm. (Cagle, 1945). For convenience in handling



PLATE 3.—The effect of shedding on the growth rings and the growth zones.

Upper. The plastron of a female collected July 4, 1941; plastron length 215 mm. The left abdominal plate shows two distinct growth rings. The light zone outside the last formed ring represents growth during the period May 1 to July 4, 1939.

Lower. The scute of the left abdominal plate has been shed. Note the change in the appearance of the growth rings which is now not distinct enough to be accurately measured.

and presenting data, I have selected the measurement of 100 mm. from this range as that size above which the great majority of males are sexually mature.

The female slider turtle becomes sexually mature at a plastral length of 165 to 195 mm. (Cagle, 1944c). All females larger than 165 mm. are here considered sexually mature.

The data for all release-recovery records and ring measurements have been consolidated in the form of tables and graphs.

THE FIRST SEASON OF GROWTH

The turtles hatch in the latter part of August or the early part of September in southern Illinois but do not usually leave the nest until the following spring. During the period in the nest there is a gradual resorption of the yolk accompanied by closure of the umbilicus and a general stiffening and hardening of the carapace and plastron. There is also a reduction of the height and an increase in the length and width of the shell. The hatchlings may leave the nest and enter the water during late March, April or early May (Cagle, 1944d).

These turtles may find the temperature still below that of their activity threshold. Such individuals float idly near the surface or cling to masses of vegetation until the temperature rises.

During the period of inactivity there is a continued reduction of the yolk mass. Two turtles collected April 27, 1940 contained yolk balls measuring 8 x 5 mm. and 4 x 3 mm. respectively. Of 21 turtles, collected May 22 to May 31, none showing any evidence of growth, 5 had no yolk present and 16 contained yolk balls 1 mm. in diameter to 2 x 6 mm., mean size 2 mm. in diameter. Three of 11 first season turtles collected June 6, 1940 had not grown and all had yolk balls approximately 1 mm. in diameter.

There is some question as to whether the yolk actually provides nourishment for the young turtle. Hildebrand and Hatsel (1926:14) believes that it does. In all the hatchlings of 7 species that I have examined the yolk is retained as a globular mass attached to the intestine and is not contained in the stomach. The researches on yolk utilization in chicks (Parker, 1929) suggest that the yolk mass may not serve as a source of nutrition. Turtles frequently feed before the yolk is completely reduced. Hatchlings collected throughout May often contained yolk balls when the intestine and stomach were filled with food.

Hatchlings showing development of plastral growth zones were first collected May 22-25, 1941, when 4 of the 44 turtles from City Lake and 18 of 20 collected at Lovett Pond showed evidence of growth, none of 17 collected from Thomas Pond, May 14, 1941 had grown. Of 11 turtles in their first season of growth collected June 6, 1940 from City Lake, 3 had not grown, 5 had grown very little, and the other 3 had grown 5.9, 4.8, and 6.9 mm. respectively. These data indicate that although growth may begin in May, the time of its initiation may vary widely in different water bodies as well as in individuals living in the same surroundings.

The annulus measurements of 60 hatchlings collected during the growing season from City Lake indicate that growth may be rapid and continuous

throughout the first season (fig. 4). The mean growth increments for the first 3 months were 4.0 mm., 6.3 mm., and 4.3 mm. A single turtle taken in September does not give a satisfactory basis for the approximation of growth increments during the last two months of the growing season. A sample of 12 collected in October showed a mean increment for the season of 25.4 mm. This is somewhat higher than the first season growth computed from the records of 55 other individuals that had completed one season of growth (table 4, fig. 8). These records indicate that the first season increase of individuals in City Lake ranges from 4.8 to 35.2 mm., mean growth 18.7 mm.

Annulus measurements indicative of the complete first season of growth are available on 31 other individuals, 11 from the Drainage Ditch and 20 from Lovett Pond. These groups had rates of growth different from that of the series from City Lake (table 4, fig. 8). The 20 turtles from Lovett Pond had grown less than one-half as much (1.9-14.8 mm.; mean, $8.75 \pm .70$) as those from City Lake and less than one-third as much as those from the Drain-

TABLE 4.—Comparison of first season growth in turtles from three areas.
Based on ring measurements of individuals having completed
one season of growth.

Area	No.	Range	S.D.	Mean	S.E.
Drainage Ditch	11	19.1-42.1	6.38	27.5	1.92
City Lake	55	4.8-35.2	7.70	18.7	1.03
Lovett Pond	20	1.9-14.8	3.16	8.75	0.70

See page 727 for key to abbreviations used in the above table.

age Ditch (19.1-42.1 mm.; mean 27.5 ± 1.92). These data demonstrate that habitat may have a highly significant effect on growth rate.

The first season growth of the Drainage Ditch turtles (fig. 7; Nos. 2898, 890, 995) was more rapid than that of City Lake turtles for the same year (fig. 5; Nos. 826, 827, 539, 844), and a similar difference is apparent for the 1938 season.

Two other sources of information on the first season of growth are the annulus measurements indicating a part of a season's growth (Table 6) and the release-recovery data (table 7). The amount of growth during the first season is best measured by the mean increment per 100 days of the first 2 size groups (20-30 and 30-40 mm.). The release-recovery records denote an increment of 13 mm., or a 43% increase; the ring measurements an increment of 14.4 mm. or a 48% increase.

The ring measurements of Drainage Ditch hatchlings indicate an increment of 15.8 mm. or a 53% increase. Lovett Pond turtles grew only 5.6 mm. per 100 days or a 19% increase. No release-recovery records are available on first season turtles in the Drainage Ditch or Lovett Pond.

The time of initiation of first season growth may be of major importance

in explaining the wide difference of increment in these 3 areas. No data are available for 1940 but hatchlings collected during the last week of May 1941 indicate that the time of growth initiation does vary in different areas. Of 40 turtles collected in City Lake only 2 exhibited measurable growth; of 15 from the Drainage Ditch, none had grown; of 20 from Lovett Pond, 17 had grown.

We might conclude that turtles from the Drainage Ditch exhibit a higher growth increment than turtles from the other two areas; but if the ring measurements of 4 first season turtles examined in 1942 be considered, a modification of this conclusion is necessary. The data on these 4 turtles (table 9) indicate a growth of 12.5-38.6 mm., mean 28.5 mm. per 100 days of the 1942 season, a growth rate substantially different than that based on ring data of

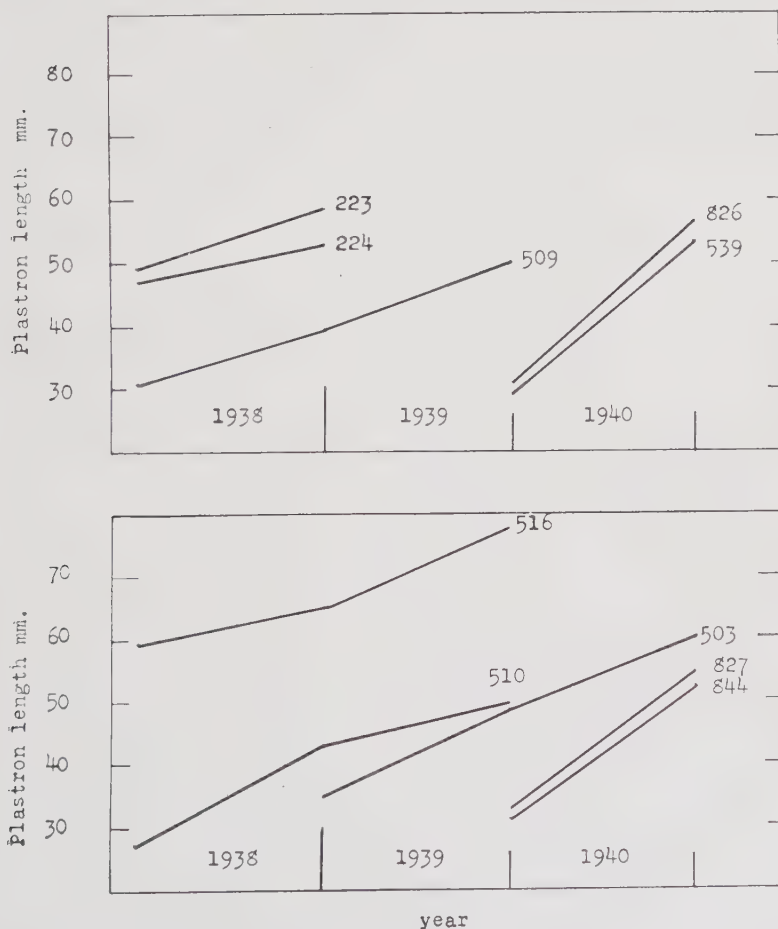


Fig. 5.—Growth of turtles in their first, second or third season at the City Lake in 1938, '39, '40.

turtles collected previous to 1942 (mean 14.4 mm. per 100 days). This increase resulted from a radical change in the biota of City Lake in 1942, subsequently discussed in this report. Thus previous to the 1942 season the Drainage Ditch turtles did have a higher rate of growth than those in City Lake but in 1942 this situation was reversed. This greater growth in the Drainage Ditch previous to 1942 was, presumably, a result of the wealth of invertebrate life present in and along the margins of the ditch. The narrow vegetation-crowded, shallow portions inhabited by the young turtles are overhung by weeds that supply a rain of terrestrial insects, which provide the main item of the young turtle's food. Such an abundance of food was not present in City Lake but would be

TABLE 5.—Growth of City Lake turtles per season. Based on annuli measurements indicating one complete season's growth.

Size group mm.	Juveniles			Males		
	No.	Inc. Range mm.	Inc. M.	No.	Inc. Range mm.	Inc. M.
20-30.....	14	10.4-33.5	20.1			
30-40.....	43	4.8-35.2	18.6			
40-50.....	7	5.5-18.0	9.3			
50-60.....	12	6.2-18.8	11.8			
60-70.....	24	7.3-18.9	12.0			
70-80.....	34	5.6-33.0	12.2	1		5.7
80-90.....	17	3.6-29.5	11.4	1		7.6
90-100.....	16	4.6-14.9	11.3	2	12.4-16.0	14.2
100-110.....	8	6.9-18.1	11.1			
110-120.....	6	8.6-28.9	15.2			
120-130.....	9	4.4-20.8	11.0			
130-140.....	5	7.1-17.5	12.9			
140-150.....	2	6.9-14.3	10.6			

See page 727 for key to abbreviations used in the above table.

expected in Lovett Pond where in normal times the shallow waters are rich in life. This pond sometimes dries during the summer months and is refilled slowly during the next spring. Such a situation may have existed in 1940; if so, it is the most likely explanation of the low growth rate in the turtles from the pond.

The growth record of a juvenile female collected from Lake Glendale emphasizes the possible influence of habitat on growth; it has only one annulus, (pl. 2) and if the age judgment based on the ring evidence is correct, this turtle had a phenomenal growth for the first season. Its plastron had increased from 31.6 mm. (as indicated by the first annuli) to a length of 110 mm., an increment of 78.4 mm. The annuli of the carapace are as distinct as those of the plastron and also indicate that the turtle is in its second season of growth. The only other explanation of this evidence is that the turtle is much older

than is indicated and has been growing continuously without forming growth zones. This would indicate a habitat in which the temperature remained fairly high and food abundant during the winter. It is difficult to concede the possibility of such a place existing in the lake or the adjacent waters. In addition one would expect the first annuli to be indistinct if the turtle were several years old; yet they were as sharply defined as those of the usual 2-3 year old turtle. Its growth for the second season of its life (47.7 mm. per 100 days) was nearly as rapid as that during the first (51.2 mm per 100 days). Five other larger individuals taken from the lake on the same date also show an unusually rapid growth.

TABLE 6.—The growth of City Lake turtles per 100 days of the season. Based on annuli measurements indicating less than one season of growth.

Size group mm.	Juveniles and females				Males			
	No.	Range mm.	M.	% inc. 100 days	No.	Range mm.	M.	% inc. 100 days
20-30.....	15	10.7-24.4	16.1	64				
30-40.....	31	9.1-42.3	16.5	47				
40-50.....	4	8.4-31.6	16.2	36				
50-60.....	12	2.5-33.0	12.3	22				
60-70.....	7	11.2-26.5	20.6	32				
70-80.....	16	2.3-17.4	9.7	13				
80-90.....	34	2.9-21.8	8.6	10	1		6.1	7
90-100.....	26	2.7-23.3	10.5	11	2	6.1- 7.4	6.9	7
100-110.....	22	2.5-34.0	11.4	10	6	3.2-18.9	8.0	8
110-120.....	16	3.2-19.7	10.3	9	3	12.3-13.2	12.7	11
120-130.....	15	2.3-22.2	12.6	10	1		8.0	6
130-140.....	7	8.3-16.7	9.2	7				
140-150.....	6	5.0-19.5	11.9	8				
150-160.....	6	2.1-12.4	7.3	5				
160-170.....	9	4.9-14.3	9.4	6				
170-180.....	3	3.9-17.0	10.2	6				
180-190.....	2	6.7- 9.0	7.8	4				
190-200.....	3	0.7- 7.1	3.7	2				

See page 727 for key to abbreviations used in the above table.

The release-recovery records yielded additional information on first season growth. Of 166 turtles in the size range 20-50 mm., most of which were in their first season of growth, released from August, 1938 to July, 1941, 24 were recovered at least once. Thirteen of these show great individual difference in growth rate. Their growth, during at least 25 days in the growing season, calculated as growth per 100 days, ranged from 0 to 30.6 mm., or from no increase at all to one of 77%. A comparison of the records of individuals released during the same period adds further emphasis to this variation. Nos. 430 and 439 both had the same plastron length and were released for similar

periods. The former grew 14 mm.; the latter, 26 mm. A possible influence on this growth was the fact that No. 430 spent the first winter of its life in the nest and No. 439 in the water. The former, released for the longest period of any turtles in this group, a total of 632 days, encompassing 19 days in the 1939 growing season (spent in the nest), the complete season of 1940 and 36 days in the 1941 season, was one of 6 hatchlings that spent the winter in a nest (Cagle, 1944d). When recovered on June 5, 1941, its ring measurements indicated that it had grown 14 mm. during the 1940 season, the only period in which it had grown. Nos. 2589 and 2627 were released during the same periods in the same portion of the lake. One grew only 1 mm.; the other, 14 mm.

TABLE 7.—The growth of turtles per 100 days of the growing season in City Lake. Determined from records of turtles released at least 20 days and showing measurable growth.

Size group mm.	Juveniles and females				Males			
	No.	Range mm.	M.	% inc. 100 days	No.	Range mm.	M.	% inc. 100 days
20-30	3	6.7-15.5	11.4	46				
30-40	9	1.7-30.6	14.6	43				
40-50	2	5.7- 7.5	6.6	15				
50-60	6	2.4- 8.2	5.4	10				
60-70	7	3.2- 9.6	6.4	10				
70-80	13	1.7-19.4	6.4	9				
80-90	23	0.4- 9.6	2.5	3				
90-100	21	0.7-12.5	3.5	4	3	1.7-18.2	7.3	8
100-110	36	0.8-28.5	4.1	4	10	0.6- 8.3	3.3	3
110-120	29	1.1-11.3	3.6	3	10	0.8- 8.6	2.2	2
120-130	21	0.7-13.1	3.7	3	13	0.6- 3.4	1.7	1
130-140	13	0.8-17.0	4.9	4	8	0.5- 3.1	1.3	1
140-150	13	0.7- 8.6	3.2	2	4	0.8- 2.2	1.6	1
150-160	5	1.0-10.3	7.0	5	5	2.2- 4.7	3.3	2
160-170	7	1.1-11.1	4.4	3	2	1.2- 1.5	1.3	1
170-180	5	2.0- 4.2	2.8	2	1		3.6	2
180-190	6	0.7-13.1	4.6	2	2	1.0- 3.9	2.4	1
190-200	5	0.5- 3.9	1.9	1	1		2.0	1
200-210	6	0.4-15.3	3.6	2				
210-220	1		1.0					

See page 727 for key to abbreviations used in the above table.

Great individual variation is also shown by the ring measurements of turtles from the Drainage Ditch in 1941 (fig. 8). These turtles were collected in about the same section of the ditch and, in all probability, had spent the first season under like ecological conditions. Similar variation of growth in turtles collected in these months is exhibited by the ranges of monthly increments in City Lake turtles (fig. 4).

It is also apparent that hatchling turtles may be isolated in a habitat where food is available for no more than a subsistence diet. Records of young captive turtles indicate that they may live for long periods without growing. Schneck (1886:897) reports keeping a young slider turtle in confinement for more than two years during which it ate freely but made no perceptible growth.

In view of the great individual variation in growth, one would not expect distinct size groups to be apparent in young turtles. One sample of 119 turtles,

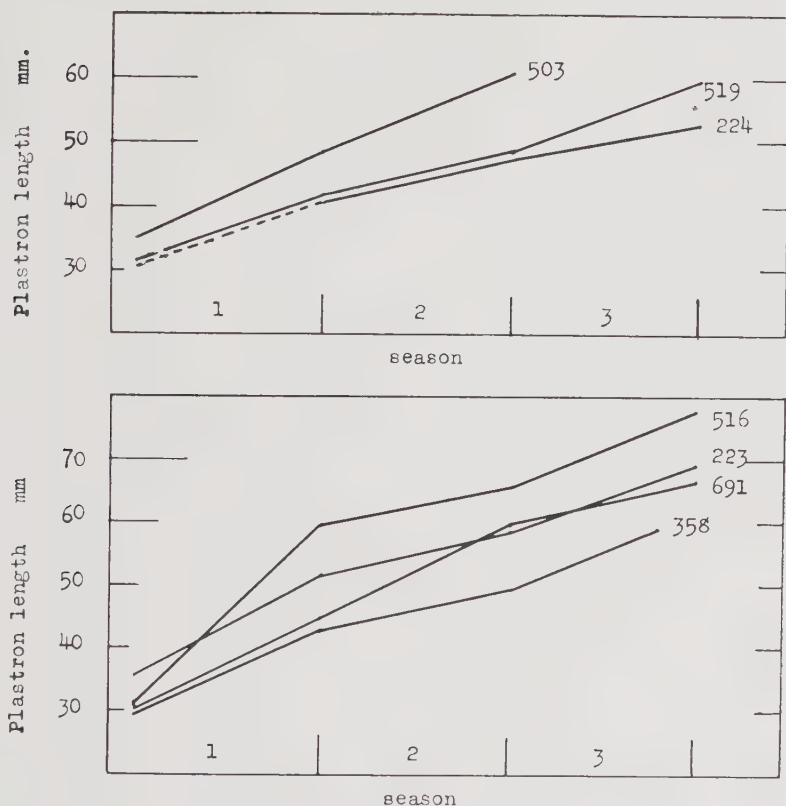


Fig. 6.—The growth of turtles in their first three seasons at the City Lake.

collected from a mudflat at City Like, June 14-20, 1941 was studied for evidence of size groups (fig. 3); five such groups are apparent, but they do not represent age groups. The age of 42 turtles in the first 3 size groups was determined; it was possible to determine the age of only one of the individuals with a plastron length greater than 64 mm. Of the first size group 30 were in their first season of growth. The second size group contained at least five individuals in their second season of growth and 3 in their third. Four of those falling in the third size group were 3 seasons old and one was 5 seasons

old. It is apparent that only the first size group represents an age group. The variation in individual growth rate results in a wide overlap in size of individuals differing several years in age.

THE SECOND AND THIRD SEASONS OF GROWTH

The only data on the second and third seasons of growth are derived from the records of those individuals that have retained 2-4 sets of annuli. From measurements of these the growth for the first 3 seasons may be determined.

The ring measurements of 7 Drainage Ditch turtles (table 10) indicate a mean growth of 15.8 mm. for the second season and 14.5 mm. for the third.

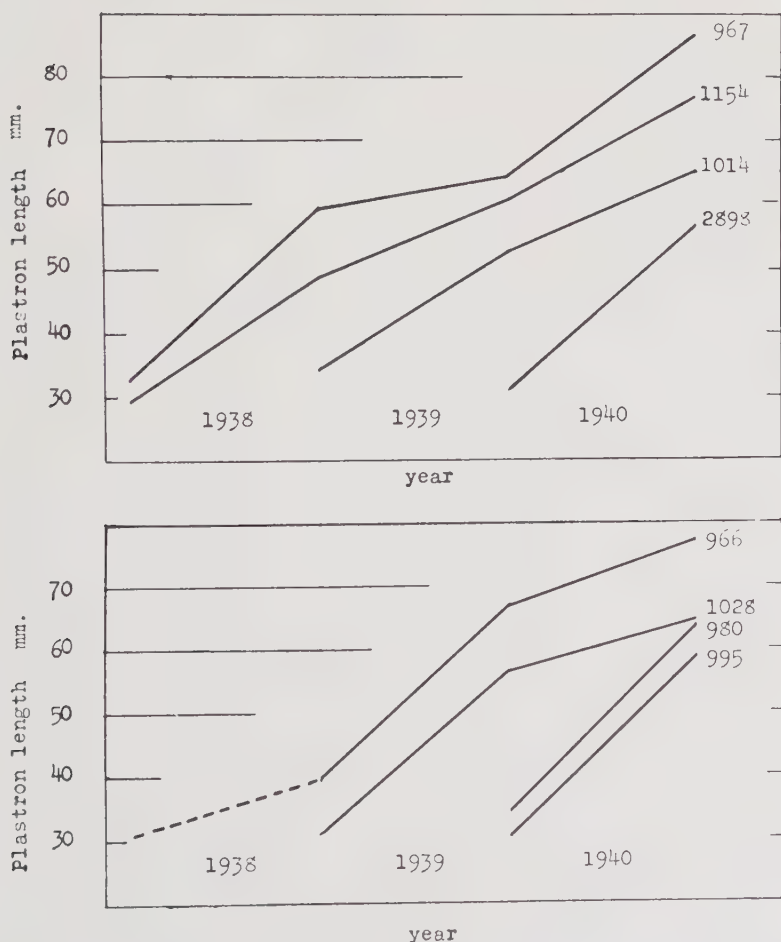


Fig. 7.—Growth of turtles in their first, second or third season at the Drainage Ditch in 1938, '39, '40.

The records of 7 City Lake turtles indicate a mean growth of 8.2 mm. for the second season, and a slightly larger amount, 10 mm., for the third (table 10).

Both sets of data indicate a smaller increment for the second season than for the first, and the records of some individuals from the Drainage Ditch and 4 from City Lake show greater increments during the third season. These increases are not as would be expected on the basis of the decreasing increment with increasing size (tables 8, 9). A difference due to the conditions of a particular season is thus suggested.

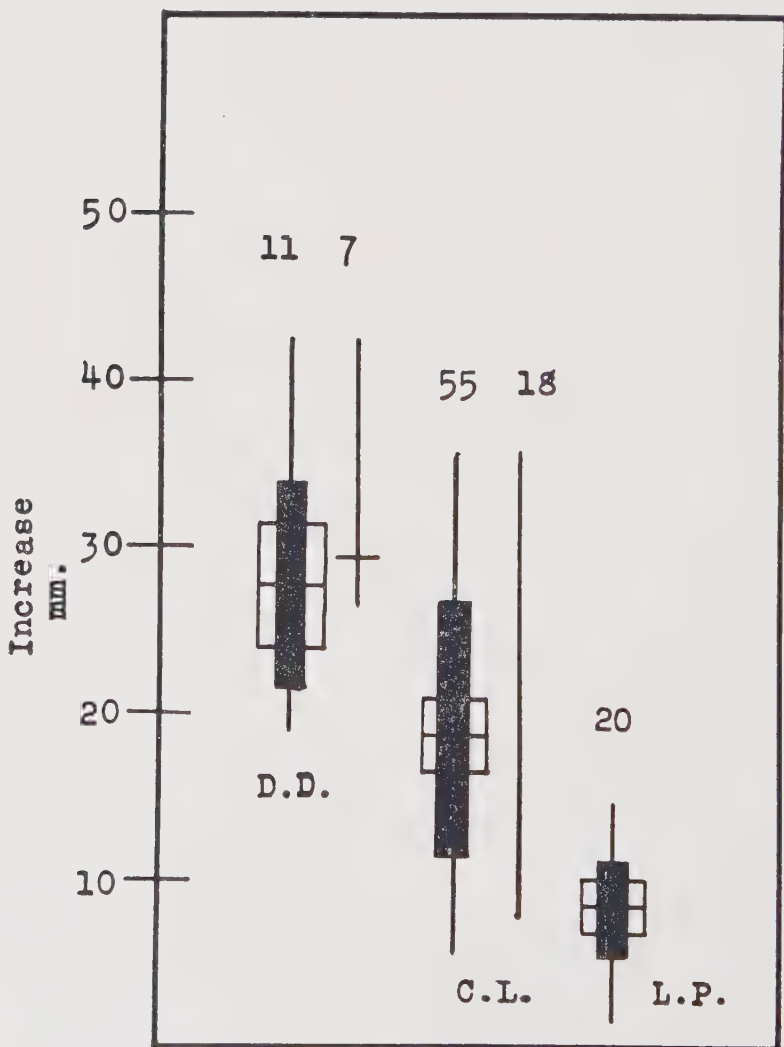


Fig. 8.—The comparison of growth in three areas during the first season.

All of the records of third season growth except that of No. 691 (fig. 6) represent growth in the 1938 season. The growth records of other turtles during this period (fig. 5) do not suggest that this season was unusually favorable for growth. All of the third season growth records of the ditch turtles represent growth for 1940, and the records of turtles released during this year (fig. 7) suggest that it may have been exceptionally favorable for growth. Thus a partial explanation is provided for these greater increments for the third season.

TABLE 9.—Growth of turtles per 100 days of the 1942 season at City Lake.
Based on annulus measurements from juveniles and females.

Size group (mm.)	No.	Range (mm.)	M. (mm.)	% inc. 100 days
20-30	2	12.5-38.6	25.5	87
30-40	2	30.3-32.7	31.5	90
70-80	1		30.2	40
80-90	6	19.1-31.0	27.1	32
90-100	6	15.0-32.9	24.8	26
100-110	6	8.6-29.4	15.8	15
110-120	3	15.0-21.9	17.3	15
120-130	1		32.7	26
130-140	1		18.2	14
140-150	1		12.8	9
150-160	1		15.4	10
160-170	1		1.9	1

See page 727 for key to abbreviations used in the above table.

Eight of 9 turtles collected June 14, 1941 were in their second season of growth, but none showed any signs of a second season growth zone. The first annuli were evident in all.

THE GROWTH OF JUVENILES OF UNDETERMINED AGE

Since the age of the great majority of turtles cannot be determined it is necessary to discuss their growth in terms of arbitrarily selected size groups. A juvenile is here considered to be any turtle having a plastron length less than 165 mm. and not showing the secondary sex characteristics of the male.

The release-recovery records of 33 juveniles released at City Lake show considerable variation in growth rates. No. 149, spending 39 days in the 1939 growing season grew 3 mm.; but in the next 1044 days (of which 408 were in growing seasons) it grew 28 mm. No. 148, released for 779 days, of which 355 were in growing seasons, increased 14 mm. in length. No. 150 increased 21 mm. in 257 days of growing season. No. 565 increased 13 mm. in 216 days. Contrary to expectation the juvenile (No. 127) that grew at the greatest rate per 100 days (11.3 mm.) was a comparatively large turtle. This individual, at liberty for 788 days of which 364 were in growing season (a portion of

the 1939, all of the 1940, and the first portion of the 1941 season), was 113 mm. in length when first released.

Although most of the juveniles released for 100 or more days in the growing season grew comparatively rapidly, some were obviously slow-growing. For example No. 480 increased only 4 mm. in 167 days of growing season. Another, No. 230, grew only 4 mm. in 205 days. Recovered twice after this record, it showed no additional growth after one period of 238 and another of 22 days. No. 231, in a period of 739 days of which 315 were in growing season, grew only 3 mm.; and No. 262, in 674 days, 250 in the season, grew only 1 mm.

TABLE 10.—Growth of turtles at the Drainage Ditch during the first 3 seasons.
Based on annuli measurements.

No.	Plastron length at birth (mm.)	Inc. first season (mm.)	Inc. second season	Inc. third season
171	32.2	26.6	24.4	
966	30.1	7.8	29.3	11.5
967	32.5	27.4	14.4	14.6
995	30.9	27.4	10.1	
1014	34.1	19.7	12.3	
1028	31.3	23.4	7.7	
1154	29.3	19.4	12.2	17.5

Growth of turtles at City Lake during the first 3 seasons.

Based on annuli measurements.

223	35.9	13.0	9.3	11.0
224	30.1	10.0	7.0	5.5
358	29.6	12.7	6.8	12.8
516	31.6	28.1	6.2	12.1
519	31.8	8.6	7.9	11.2
691	30.5	14.1	14.6	7.4
2599	29.2	23.9	6.1	

See page 727 for key to abbreviations used in the above table.

These records can but be compared by reducing them to an arbitrary standard of time interval. The growth of all City Lake juveniles was computed as growth per 100 days of the growing season (table 7). It was found that each successively larger group has a smaller increment and thus a correspondingly smaller percentage increase in length. This decline in growth rate is most rapid in the first 7 groups in which the average increment drops from 11.4 mm. to 2.5 mm. The maximum growth per 100 days of the season, 30.6 mm., was made by an individual in its first season of growth. Those groups in the 80-150 mm. range show a somewhat uniform increment. Of 246 juveniles

released 20 or more days in the growing season 45 (18%) showed no detectable increase. The percentage of juveniles not showing increase is highest (44%) in the size group 150-160 mm. and lowest (0%) in the groups 20-30 and 40-50 mm.

The release-recovery data available for Drainage Ditch turtles demonstrate that they have a higher rate of growth than those of City Lake. The most rapidly growing individual (No. 2297), released for 525 days, grew 31 mm. in the 283 growing season days. None of 7 juveniles grew less than 18 mm. in 283 days or 6.3 mm. per 100 days.

A comparison of the records of 2 of the larger juveniles with a sample from City Lake shows that those in the same size range (130-160 mm.) grew an average of 4 mm. in City Lake and an average of 8.7 mm. in the Drainage Ditch (table 11).

TABLE 11.—Growth per 100 days of the growing season as calculated from release-recovery data. (Turtles 130-220 mm. in length).

Sex	City Lake			Drainage Ditch		
	No.	Range (mm.)	Mean	No.	Range (mm.)	Mean
j j	24	0.5-17.0	4.0	4	6.3-10.9	8.7
♀ ♀	31	0.3- 9.2	3.9	11	0.3-14.2	4.2
♂ ♂	19	0.5- 4.7	2.3	5	0.7- 6.0	2.8

See page 727 for key to abbreviations used in the above table.

Annulus measurements were also used in the analysis of juvenile growth (tables 5, 6, 8, 9). A greater number of turtles showing little growth is to be expected in the larger size groups and thus annulus measurements are comparatively few in these groups. That the minimum growth for each size group above the 30-40 mm. group is zero, each successively larger group having a greater number showing no growth, is suggested by a sample from the Drainage Ditch.

None of the City Lake turtles with a length greater than 150 mm. showed sufficient growth to be detected by ring measurements. The increments for each size group for one complete season are quite uniform in those turtles larger than 60 mm. (increment average range from 10.6 to 15.2 mm. in the plastral size range 50-150 mm.). The individual showing the maximum increase for one season (35.2 mm.) was in its first season of growth.

Ring data for a complete season's growth in turtles from the Drainage Ditch (table 12) indicate a higher increment in most size groups than for comparable ones in City Lake. That large turtles in the Drainage Ditch continue to grow relatively rapidly is indicated by the fact that those with lengths greater than 160 mm. (adult females) continue to form distinct rings. This is in decided contrast with the situation in City Lake. This difference is fur-

ther demonstrated in the higher maximum increments in most of the Drainage Ditch size groups.

The data on turtles from City Lake in terms of growth per 100 days of the season determined by ring measurements are somewhat different from those based on release-recovery procedures (table 8). As expected, the ring data, because of the limitation on minimums determined, indicate higher increments for each group than do the release-recovery data. Each series does, however, demonstrate the change in rate in the first few size groups. Thus on the basis of release-recovery data the 46% increase in the size group 20-30 mm. decreases to 9% in the 70-80 mm. group. Succeeding groups of juveniles show a continued percentage decrease (2 to 5%). The two other sets of data show a similar trend.

The annulus measurements of Drainage Ditch turtles were also arranged on the basis of growth per 100 days of the season (table 12). These data may be compared with those computed by the same method for City Lake turtles (table 8).

THE GROWTH OF MALES

The release-recovery records of males in both City Lake and the Drainage Ditch suggest that their growth is slower than that of juveniles and females of the same size. Of 82 males released 20 or more days in the growing season 23 (28%) did not grow one millimeter; 45 (18%) of 246 juveniles and 12 (28%) of 42 adult females did not grow one millimeter. The growth records of adult males (table 8) indicate an average increase per 100 days of the growing season of 2.7 mm. The average growth of juveniles for a similar period was 6.5 mm.; of females 3.2 mm. (table 8). The ring measurements yield a similar result (tables 5, 6, 9, 12).

The maximum growth as determined by release-recovery methods for an adult male in City Lake was 8.6 mm. per 100 days of the season. This is considerably higher than the maximum (5.6 mm.) displayed in 7 males released in the Drainage Ditch.

The mean growth based on release-recovery records of males at City Lake was 1.8 mm. per 100 days; of males at the Drainage Ditch 2.7 mm. Of 82 males released for 20 or more days in the growing season at City Lake 23 (28%) did not grow; of 398 Drainage Ditch males examined for growth by annulus measurements 295 (74%) had no evidence of growth, 79 (20%) had grown slightly, 24 (6%) showed measurable growth.

The percentage of the Drainage Ditch males showing no evidence of growth in the plastral annuli increases in successively larger size groups. Thus in the group 100-110 mm., 21% showed no growth, 29% slight growth, and 50% distinct growth; in size group 160-170 mm., 84% showed no growth, 14% slight growth, and only 2% distinct growth. None of the males larger than 190 mm. yielded evidence of recent growth. The decline of growth rate in the larger males is also demonstrated by all other records (tables 8, 13).

The release-recovery records of some individuals are of special interest. One, released 664 days, of which 240 were in growing season, grew only 2 mm. Another, released 740 days, 316 in growing season, grew only 1 mm.

Some adults grew as rapidly as some juveniles of the same size. One of 112 mm. plastral length, grew 13 mm. in 784 days, 360 of which were in the season. No. 302, 125 mm. plastral length, grew 7 mm. in 725 days, of which 302 were in the growing season.

These data also suggest differences in growth from season to season. No. 396, recovered 3 times, did not change in length during the first 625 days (201 in growing season) but grew 2 mm. in the following 84 days. No. 285 recovered 3 times, did not grow during 2 periods of 111 and 80 days in season, but in a subsequent period of 48 days it increased 2 mm.

All of the males released in the Drainage Ditch grew at least 2 mm. in the interval of release (minimum 93 days in season). They ranged in growth .7 mm. to 5.6 mm. increase on the 100-day basis.

The growth records of males at City Lake show a 3 to 8% increase in length per 100 days in the 85-110 mm. group and a subsequent drop in larger males to a 1 to 2% increase per 100 days of the season (table 8). It should be reemphasized that these data represent measurable growth and do not include the great number showing less than 1 mm. increase.

THE GROWTH OF FEMALES

Adult females were few in City Lake and recoveries were correspondingly rare. The 42 records available show a wide range in growth (table 5) per 100 days of the growing season. Of these, 12 did not grow when released 20 or more days in the growing season; the maximum growth per 100 days of the season was 15.3 mm. The mean increments of almost every size group are higher than those of males of the same groups and lower than those of juveniles. The maximum percentage increase per 100 days (3%), was based on individuals of which some may have been immature. Groups larger than 170 mm. showed 1 to 2% increase.

The release-recovery data on some females indicate that an individual may exhibit radical differences in growth in different seasons. No. 20 grew 4 mm. in 166 days, most of which were in the 1939 season and 2 mm in 106 days of the 1941 season but showed no detectable increase during 114 days of the 1940 season. Similarly another, No. 75, grew 14 mm. in only 91 days of the first part of the 1939 season but only 1 mm. in 61 days of the latter part of the same season.

Six females released at the Drainage Ditch for 535 days, of which 283 were in growing season, all showed a similar growth rate to those in City Lake. The increase for the 283 days ranged from 1 to 9 mm. or from approximately .4 mm. to 3.2 mm. per 100 days of the season.

The few ring measurements (tables 5, 6) available on females from City Lake indicate again a lower rate of growth than for juveniles (2 to 8% increase per 100 days for the females, 9 to 64% for juveniles). The ring measurements of the Drainage Ditch females show a like difference in rate (2 to 5% increase in females, 7 to 52% for juveniles).

Of the 408 females examined for growth on the basis of rings in the Drainage Ditch, 45% showed no evidence of growth, 45% had grown slightly and 10% exhibited measurable growth.

TABLE 12.—Growth of Drainage Ditch turtles. Based on annulus measurements indicating one complete season's growth.

Size group	Juveniles and females					Males				
	No.	Inc. per season range (mm.)	Inc. M.	Inc. per 100 days (mm.)	% inc. per 100 days	No.	Inc. per season range (mm.)	Inc. M.	Inc. per 100 days (mm.)	% inc. per 100 days
20-30.....	4	19.1-26.3	17.5	11.4	46					
30-40.....	11	16.2-42.1	27.7	18.1	52					
40-50.....	4	12.2-21.4	17.0	11.1	25					
50-60.....	9	4.4-15.9	11.7	7.6	14					
60-70.....	28	3.0-39.0	14.9	9.7	15					
70-80.....	38	1.7-31.6	14.7	9.6	13					
80-90.....	59	3.4-33.0	12.0	7.8	9		10.6-19.5	15.0	9.8	12
90-100.....	43	2.6-34.2	11.0	7.2	8		7.6-18.0	13.1	8.5	9
100-110.....	25	3.5-44.2	12.3	8.0	8		1.6-16.8	9.4	6.1	6
110-120.....	28	0.4-32.0	12.1	7.9	7		5.1- 7.1	6.1	4.0	4
120-130.....	22	3.7-30.5	13.7	8.9	7					
130-140.....	19	0.9-40.7	17.0	11.1	8	1		19.2	12.5	9
140-150.....	20	1.6-40.3	15.1	9.9	7	4	7.1-13.7	9.4	6.1	4
150-160.....	5	0.5-32.4	14.6	11.7	8	1		10.6	6.9	5
160-170.....	3	15.1-22.7	17.8	11.6	7	2	10.1-10.5	10.3	6.7	4
170-180.....	10	7.0-24.4	12.4	8.1	4					
180-190.....	8	7.4-19.3	11.7	7.6	4					
190-200.....	4	9.1-18.0	14.1	9.2	5					
200-210.....	2	1.9-12.1	7.0	4.6	2					

See page 727 for key to abbreviations used in the above table.

Discussion

Differences in the growth rate of turtles, occupying different habitats are conspicuous (table 4, fig. 8). The population of the Drainage Ditch consisted of turtles growing at a faster rate than those of City Lake, and the average size of the adults of the ditch population was larger than the average size of the adults in the lake population (mean size of males: 161 mm. in the ditch, 114 mm. in the lake; mean size of females: 193 mm. in the ditch, 180 mm. in the lake). This size difference is a result of the greater age of the population, and of the higher growth rate of the ditch turtles. Individuals of the ditch population move between the ditch and the adjacent ponds, lakes, and swamps as well as the Mississippi River (Cagle, 1944b) and many of the large adults are probably older than the ditch. The greater age of these large turtles is indicated by eroded jaws, thickened horny layers of the carapace, pitted carapace, and almost complete obscuration of color pattern. Comparatively few individuals from City Lake showed evidences of old age.

The greater rate of growth in the ditch turtles is primarily a result of two factors, the shallowness of the water with resultant higher temperatures, and the wealth of available food. Although the water level of the ditch may become very low so that portions of its bed become dry in late summer, there are usually several inches to a few feet of water in the ditch during most of the growing season. The shallow water remains quite warm, and the metabolic rate of the turtles inhabiting it is therefore undoubtedly higher than those of the turtles in City Lake.

The great variation in growth of individuals in each region may result from the fact that individual turtles tend to remain in a given section of the ditch or the lake until forced to move by radical ecological changes. I have demonstrated (1944b) that City Lake supports 3 population groups, each of which tends to remain in one portion of the lake or the adjacent ponds. Differences in the water temperatures, availability of food, and basking sites may result in different growth rates of individuals inhabiting these areas.

The influence of habitat on growth is further shown by the records of turtles collected from Lake Glendale. These indicate a much greater rate of increase than do those of turtles examined from other region. Analysis of the growth of 10 turtles collected in 1942 indicates that the per cent increase per 100 days in plastral length varied from 4 per cent in a large male to 162 per cent in a juvenile. This lake was first flooded in 1940. Just previous to the closing of the water outlet members of the Illinois Natural History Survey poisoned the small streams emptying into the lake bed. A few of the fishes from these waters survived and the lake was stocked with a small number of fish. The few turtles entering the lake thus had an abundance of food available and little competition.

A single individual from Lake Springfield, in central Illinois suggests that the population there may consist of rapidly growing individuals. This adult female, with a plastron length of 260 mm., was the largest of the turtles examined from Illinois. Although exceptionally large, it had the smooth plates, bright colors, distinct pattern and sharp jaws of a relatively young individual.

It was certainly not near senility as the oviducts contained 20 eggs and the ovaries were heavy and crowded with large follicles.

The effect of a change in habitat on growth was noted when the growth of City Lake turtles was determined for 1942. In October of 1941 the lake reached its lowest level since its construction in 1926. From spillway level

TABLE 13.—Growth records of turtles, recovered during the 1942 season, which indicate growth for previous seasons.

No.	Sex	Date	Days in season	P. l. (mm.)	Inc. (mm.)	Inc. per 100 days (mm.)	% inc. 100 days
128.....	j ♀	6/9/39		101			
		7/27/39	48	102	1	2.1	2
		5/5/41	223	104	2	0.9	1
		6/6/42	185	116	12	6.5	6
129.....	j ♀	7/27/39		104			
		7/10/40	135	105	1	0.7	1
		8/3/40	24	105			
		6/6/42	248	116	11	4.4	4
149.....	j	6/18/39		73			
		7/27/39	39	76	3	7.7	10
		6/6/42	408	104	28	6.9	9
		9/9/42	95	119	15	15.8	15
143.....	j ♀	6/18/39		117			
		6/6/41	294	156	39	13.3	11
		9/9/42	248	165	9	3.6	2
215.....	j ♀	7/27/39		117			
		9/17/40	205	120	3	1.5	1
		6/6/42	203	132	12	5.9	5
232.....	j ♂	7/28/39		65			
		6/16/41	264	74	9	3.4	5
		8/1/41	46	74			
		9/1/42	184	103	29	15.8	2
287.....	♀	8/12/39		182			
		6/30/40	110	183	1	9.1	5
		6/6/42	129	200	17	13.1	7
315.....	j ♀	8/11/39		127			
		5/5/41	209	128	1	0.5	4
		8/6/41	93	133	5	5.4	4
		9/9/42	187	143	10	5.3	4
384.....	j ♀	8/27/39		104			
		6/19/40	84	105	1	1.2	1
		9/11/42	390	143	38	9.7	9

See page 727 for key to abbreviations used in the above table.

(450 acres) in early spring it dropped steadily with slight fluctuation to an average depth of a few inches covering about 10 acres. During mid-October it was drained except for 2 small pools and did not refill to spillway level until April of 1942. During the period of low water vegetation grew luxuriantly on the exposed bottom, and in the spring and summer of 1942 all the shallow areas of the lake developed extensive beds of aquatic plants not previously present in the lake.

During the period when the water level was very low the greater part of the turtle population moved to adjacent ponds and streams but returned when the lake was again flooded (Cagle, 1944b).

The radical change in the amount of vegetation in the lake was reflected by a change in the growth of the turtles. The ring measurements of 31 juveniles indicate that they were growing more rapidly in 1942 than individuals of the same size in the previous seasons. Thus 4 individuals in the 20-40 mm. group (all in their first season of growth) were growing at a rate of 12.5 to 38.6 mm., mean 28.5 mm. per 100 days of the season. Forty-six individuals of the same size range collected in previous seasons grew at a rate of 9 mm to 42 mm., mean 16.3 mm. A faster rate of growth than in earlier years was indicated by the ring measurements of the individuals in each group except the 160-170 mm. one (compare the percentage increase per 100 days of each size group in table 6 with that of each size group in table 9). Furthermore, these turtles were growing more rapidly than those in the Drainage Ditch during previous seasons as is seen by comparison of the percentage increase per 100 days of each size group in table 12 with that of each size group in table 9.

Because of the wide variation of individual growth, the records of these individuals whose growth can be determined for the 1942 season as well as for previous seasons present the better picture of the change in growth rate. Two of the 31 turtles whose rings were studied in 1942 had 2 or more series of rings from which growth for previous seasons could be computed. One, a juvenile female 119 mm. in length, had grown at a rate of 7.8 mm. per 100 days in 1941 but at a rate of 22.5 mm. per 100 days in 1942. A second juvenile, length at time of collection 107 mm., grew at a rate of 6.6 mm. per 100 days in 1937, its first season of growth; a rate of 8.6 mm. per 100 days in 1938; and 8.7 mm. in 1939. In 1942 it grew at a rate of 21.9 mm. per 100 days, a greater rate than in any other season of its life, including the first season when growth is usually the most rapid.

Some of the turtles collected in 1942 had been recovered on previous occasions, and it is therefore possible to compare their growth in 1942 with that of previous years (table 13). The decrease in growth rate of two of these turtles was probably the result of the approach of sexual maturity since the plastron length of the female (No. 143) at the time of collection in 1942 was 165 mm. and that of the male (No. 232) 103 mm. Seven had grown more rapidly in 1942 than in previous years. Some of the rate increases were exceptionally large. In 1939, No. 149 increased in length at the rate of 10% per 100 days; in 1941, at the rate of 9%; but, in 1942, when, on the basis of

the decreasing rate with increasing size previously demonstrated, one would expect a marked decrease in rate, it increased in length at the rate of 15% per 100 days. The growth of these 7 individuals during 1942 was more rapid than that of any other of the same size group in previous years.

These data indicate that radical differences may exist in the growth rate of turtles living in different habitats within a region small enough to have no significant variation in the length of the growing season.

They further suggest that turtles are capable of very rapid growth and that environmental factors affect the rate of increase. The rate of growth responds quickly to a change in environmental conditions.

Summary

METHODS

1. A measuring device suitable for accurate measurement of the carapace and plastron is described.

2. It is demonstrated that measurements of annuli provide valid data for growth analysis, providing growth data for previous seasons, and delimiting the period in which growth, detected by other procedures, occurred.

ANNUAL ACTIVITY CYCLE

3. The normal activity in nature is limited to the temperature range of approximately 10° to 37° C.

4. Turtles are active in the winter only as water temperatures permit. In southern Illinois activity begins about the last of April or the first of May. There is some decline of activity in midsummer and a subsequent increase in August and September. Feeding ceases in early October.

5. The growing season in southern Illinois extends from approximately May 1 to October 1, a period of 153 days.

ANNULUS FORMATION

6. Annuli are usually formed annually and represent the cessation or slowing of growth during the winter months.

7. Annuli are of little value as age indicators since they disappear at a relatively early stage.

SHEDDING

8. Shedding may take place at any time but usually occurs in late summer.

9. Shedding probably occurs more frequently in young turtles than in adults.

10. Shedding has little or no effect on growth.

FIRST SEASON OF GROWTH

11. Growth for the first season is extremely variable. One individual grew only 1.9 mm.; the maximum growth was 78.4 mm.

12. Turtles examined from three areas exhibited radical differences in growth for their first season.

SECOND AND THIRD SEASONS OF GROWTH

13. Growth during the second and third seasons is generally less rapid than during the first, but seasonal differences may reverse this rule.

GROWTH OF JUVENILES (OF UNDETERMINED AGE)

14. There is a progressive decrease in rate of growth with increase in size.

15. Juveniles in each size group exhibit wide variation in the growth rate.

GROWTH OF ADULTS

16. After the attainment of sexual maturity results the growth rate decreases.

17. Growth is very slow in most adults; many showed no evidence of growth when released for long periods.

18. There is a progressive slowing of the growth rate with increase of size.

19. Adult males grow more slowly than females of the same general size.

GENERAL

20. The growth rate is potentially very rapid in juveniles and young adults and is responsive to and limited primarily by ecological factors.

21. Individuals of approximately the same size and living under similar ecological conditions exhibit wide differences in the rate of growth.

22. The largest male collected was 186 mm. in length; mean size of adult males was 135.4 mm. The largest female collected was 260 mm. in length; mean size of adult females was 189.1 mm.

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A KEY TO ABBREVIATIONS USED IN THE TABLES.

C.l.—Carapace length
C.w.—Carapace width
Ht.—Height
Inc.—Increase
M.—Mean

No.—Number of items, or identification
number of an individual
P.l.—Plastron length
P.w.—Plastron width
S.D.—Standard deviation
S.E.—Standard error

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